HYMENOPTEROUS PARASITES IN EGG SACS OF SPIDERS OF THE GENUS PARDOSA (ARANEIDA, LYCOSIDAE)

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With 2 text-figures, 4 graphs and 3 plates

ABSTRACT

The occurrence of two hymenopterous egg parasites, *Gelis* spec. (Ichneumonidae) and *Acolus krygeri* Kieffer (Proctotrupidae), in egg sacs of spiders of the genus *Pardosa* (Araneida, Lycosidae) in the Netherlands is described.

Gelis spec. develops in the spider egg sac. All spider eggs are either eaten or destroyed by the larvae. Only a small proportion of *Pardosa* egg sacs is parasitized by *Gelis:* ± 140 out of ± 5000 egg sacs. In some species and at some sampling sites the degree of parasitism can be rather high, up to 42.6%.

Acolus krygeri develops in a single spider egg. Only a proportion of spider eggs in an egg sac is parasitized, the other eggs develop into young spiderlings normally.

Acolus krygeri occurs in the Netherlands only on the Frisian island Schiermonnikoog. This species parasitizes mainly egg sacs of *Pardosa nigriceps* (Thorell), viz., to about 70%, with a mean number of 10 parasites per sac; this means that 30 to 60% of the spider eggs are attacked. To a lesser extent egg sacs of *P. pullata* (Clerck) are attacked.

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INTRODUCTION

In order to study the egg production of spiders of the genus *Pardosa* (Lycosidae) in the field, a large number of female spiders carrying egg sacs have been collected. In some samples a number of eggs sacs contained larvae of a hymenopterous parasite, *Gelis* spec. (Hymenoptera, Ichneumonidae). In other samples, collected on the Frisian island Schiermonnikoog, larvae of *Acolus krygeri* Kieffer (Hymenoptera, Proctotrupidae) were found in spider eggs. A study of the interrelation between parasites and spiders was initiated, in order to establish the effect of parasitism on egg production in spiders of the genus *Pardosa*. The results of this study are presented in this paper.

Life history of *Pardosa* in the Netherlands

In early spring the juvenile spiders moult to the adult stage (March-April). About one month later the females construct egg sacs, which are carried around on the spinnerets (May-June). Again after about one month the juvenile spiders emerge. The females can produce a second egg sac (July-August), and very seldom, a third one. Most of the juvenile spiders reach the penultimate stage before winter. For more detailed description of the life history of *Pardosa* may be referred to Vlijm et al. (1963).

Eight species of the genus *Pardosa* can be found in reasonable numbers in the Netherlands: *P. amentata* (Clerck), *P. lugubris* (Walckenaer), *P. pullata* (Clerck), *P. prativaga* (L. Koch), *P. nigriceps* (Thorell), *P. purbeckensis* F.O.P.-Cambridge, *P. monticola* (Clerck), and *P. palustris* (Linnaeus).

The parasites

As is said above, we have to deal with two types of egg parasites.

1. *Gelis* spec. (Hymenoptera, Ichneumonidae).

The members of the genus *Gelis* are ant-like insects; the females are wingless, the males have wings; their length is 2 to 2.5 mm (Pl. I Fig. A1 and A2). The species are rather difficult to identify, and therefore they are dealt with as a genus. The larvae develop in spider egg sacs in such a way, that no spiderlings can emerge from the parasitized egg sac; the larvae consume all the spider eggs or, if not all eggs in the sac are eaten, the remaining eggs are destroyed by the prepupae.

2. *Acolus krygeri* Kieffer (Hymenoptera, Proctotrupidae, Scelioninae).

These are rather small insects (length ± 1.2 mm). The females are wingless, the males have wings (Pl. I Fig. B1). The larvae develop in a single spider egg. Non-parasitized spider eggs develop normally. The species was recorded by Kryger from Denmark, obtained from eggs sacs of *Lycosa* spec., especially *Lycosa picta* (the latter is probably synonymous with *Arctosa perita* Latreille).

MATERIAL AND METHODS

All samples of *Pardosa* females with egg sacs were collected by hand on sunny days. In this way one only catches spiders, that are active upon the vegetation. However, there is reason to believe that on sunny days nearly all females are out on the vegetation, exposing their egg sacs to the sun.

The parasites used for experimental purposes were obtained by collecting *Pardosa* females with egg sacs from localities, where in former years a reasonable number of egg sacs were found to be parasitized. The spiders were kept in cages and as soon as parasites emerged, these were transferred to small glass jars and supplied with water and honey. The temperature was kept at 20 to 25°C.

Previously a number of *Pardosa* females were retarded in their development by keeping them under low temperature conditions. Thus they constructed their first egg sac after the emergence of the first egg sacs of spiders in the field, and just in time to supply the parasites in the experiments with fresh spider egg sacs.

RESULTS

1. Gelis spec.

A. Field observations

Larvae of *Gelis* spec. have been found in egg sacs of all *Pardosa* species in the Netherlands, except in *P. palustris.*

In table 1 all available data are presented. It is evident from this table that the degree of parasitism is highly variable among the different *Pardosa* species. In nearly 35% of the samples *Gelis* larvae were found. The degree of parasitism of *Gelis* in *Pardosa* egg sacs in general is not very impressive. Only 139 out of 5116 egg sacs were found to be parasitized. On 65% of the sampling sites, however, we never found parasitized egg sacs, even though a high number of sacs were collected on these sites.

When we consider the number of parasitized egg sacs in those samples where parasites were found, it is evident that the degree of parasitism can be rather high (Table 2). The highest parasitism (e.g. 42.6% in *P. amentata)* was found in samples of second egg sacs. Moreover, in *P. purbeckensis* and *P. pullata* only the second egg sac was found to be parasitized. It is not clear whether the first egg sac in these two species is not parasitized at all. More likely the number of parasitized egg sacs is so low, that they have not been met with in the samples. It should be noted that we did not succeed in taking samples of second egg sacs of all species and on all sampling sites.

Table 1. General impression of the occurrence of *Gelis* larvae in egg sacs of species of *Pardosa* at different sampling sites

Spider species	Number of egg sacs	Number of samples	Number of samples with parasitized egg sacs	Number of sampling sites	Total number of parasitized egg sacs
P.amentata	1006	16	9 (56.3%)	6	53
P.lugubris	601	6	3 (50.0%)	3	31
P.pullata	791	17	6 (35.3%)	2	13
P.prativaga	147	2	1 (50.0%)	2	12
P.nigriceps	1324	18	5 (27.8%)	2	9
P.purbeckensis	609	11	2 (18.2%)	3	20
P.monticola	445	7	1 (14.3%)	3	1
P.palustris	193	3	- -	2	-
Total	5116	81	28 (34.6)	12 1)	139

1) Some sampling sites are the same for several species

Table 2. Mean percentage of parasitism in samples of *Pardosa* species, where *Gelis* larvae were found

	Mean % of parasitized egg sacs	Number of samples	Highest and lowest % found
P. amentata	9.7	9	42.6 — 0.7
P. lugubris	8.1	3	22.6 — 2.0
P. pullata	8.9	6	16.7 — 2.1
P. nigriceps	3.7	5	5.9 — 1.8
P. purbeckensis	14.7	2	25.7 — 3.7
P. monticola	2.0	1	2.0
P. prativaga	8.0	1	8.0

These considerations do suggest that *Gelis* presumably is much more widespread than is indicated in table 1.

Number of larvae in the spider egg sac.

The interrelation between the number of spider eggs per egg sac and the number of larvae of *Gelis* is shown in table 3. The size of spiders with parasitized egg sacs did not differ from that of spiders with normal egg sacs. Thus there is no reason to assume that the parasitized egg sacs contained different numbers of spider eggs, this number being correlated with the size of the mother spider (cf. Petersen, 1950). Moreover, the number of eggs could be counted when the *Gelis* larvae were very young, and this

Table 3. Mean number of *Gelis* larvae per egg sac found in samples of the first (1) or second (2) egg sac of different *Pardosa* species, and the calculated mean number of spider eggs available to one *Gelis* larva in the different samples

Spider species	First or second egg sac	Mean number of spider eggs per egg sac	Mean number of Gelis larvae in parasitized egg sacs	Number of spider eggs available to one Gelis larva	Number and percentage of parasitized egg sacs in the sample
P.pullata	2	16.0	1.8 ± 1.17	8.9	6 (21.6)
P.purbeckensis	2	26.7	3.1 ± 0.87	8.6	18 (26.1)
P.amentata	2	49.7	4.9 ± 1.94	10.1	23 (42.6)
P.lugubris	1	40.5	5.1 ± 2.35	7.4	19 (22.6)
P.amentata	1	74.4	6.6 ± 4.28	11.3	7 (6.7)
P.prativaga	1	48.9	7.0 ± 2.37	6.4	12 (10.2)
P.amentata	2	54.1	7.6 ± 3.10	7.1	7 (13.0)
P.amentata	1	65.7	10.3 ± 3.24	6.4	8 (8.9)

number did not differ from the numbers in non-parasitized egg sacs. However, as a rule, it is not possible to count the number of spider eggs in a parasitized egg sac. Therefore the mean number of spider eggs in not parasitized egg sacs of the same samples is chosen as an estimate of the spider eggs available to the larvae in a parasitized egg sac.

There clearly is a relation between the number of host eggs and the number of *Gelis* larvae. It is striking, that the number of larvae is highest, when the percentages of parasitized egg sacs in the samples are lowest. This is, however, a consequence of the fact, that second egg sacs, containing fewer eggs than the first egg sacs, have a higher degree of parasitism. The number of eggs available to one *Gelis* larva ranges from 6.4 to 11.3.

Table 4. Mean number of old and young *Gelis* larvae per egg sac in one sample of *Pardosa lugubris* and one sample of *P. prativaga*

Spider species	Young larvae	Number of egg sacs	Old larvae or pupae	Number of egg sacs
P. lugubris	4.7 ± 1.88	12	5.6 ± 2.38	11
P. prativaga	6.5 ± 2.43	6	7.5 ± 2.43	6

In two samples of *Pardosa lugubris* and *P. prativaga,* collected in the same period, it was possible to compare egg sacs with very young *Gelis* larvae (in that stage the spider eggs are not yet damaged), with egg sacs containing old larvae or pupae. The results are shown in table 4. The mean numbers of old and young larvae were not significantly different in those samples. Therefore it may be concluded, that the number of *Gelis* eggs, deposited in one egg sac, is proportional to the number of spider eggs in these egg sacs.

B. Laboratory observations

A number of spiders carrying egg sacs was collected in the field and kept in cages. Every day the cages were searched for parasites. A total number of 49 specimens was collected that way : 28♂ and 21♀ (Table 5). The slight predominance of males over females is not statistically significant. The parasites were kept in glass tubes, together with a small sponge soaked in water and honey.

After emergence the males and females mated very soon (duration of the copulation: 5 - 10 minutes); consequently, the females were able to lay eggs within 1 or 2 days after emergence.

Table 5. The number of *Gelis* males and females emerged from different samples of *Pardosa amentata* females with egg sacs, collected in the field

Spider species :	Number of egg sacs	Total number of *Gelis* in the sample	
P. amentata		♂	♀
	30	4	6
	90	10	5
	70	7	3
	11	4	3
	40	3	4
		—	—
Total		28	21

Parasitizing of the spider egg sac.

When a *Pardosa* spider carrying a fresh egg sac is put in a tube together with a *Gelis* female, the latter becomes very active. After about 10 minutes the *Gelis* female jumps on the egg sac, walks around on the surface of the egg sac for a few minutes and then pierces the egg sac with her ovipositor (Pl. I Fig. B2). The eggs are mostly deposited at the edge of the egg sac, where the two halves of the sac are joined together (for a description of the egg sac, cf. Vlijm et al., 1963). After egg laying the *Gelis* female leaves the egg sac or sometimes pierces the sac at another point. The number of parasite eggs found in the egg sacs in these experiments varied between 1 and 7.

An easier method to obtain parasitized egg sacs is to remove the sac from the female spider and put it in a tube with the parasite. It takes less time then for the parasite to mount the egg sac than in the case of a spider running around with its egg sac. After being parasitized, the egg sac be returned to the owner; in all cases it was readily accepted by the female spider.

Development of the *Gelis* larvae.

The development of the larvae was studied by keeping larvae separately with some spider eggs, which were replaced by fresh ones every two days, in "cages" (small glass rings with some moist plaster of Paris on the bottom and sealed with a piece of filter paper, Fig. 1). The results were compared with data of larvae developing normally

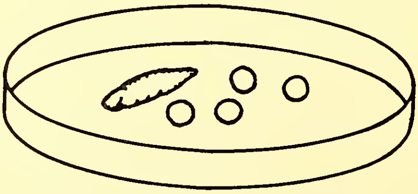


Fig. 1. Glass "cage" with one *Gelis* larva and some spider eggs

within a spider egg sac. This procedure had to be followed since the *Gelis* larvae are lost for the experiment when egg sacs are opened for inspection and determination of the development of the larvae. Moreover, in the small cages one can easily assess the feeding rate of the larvae.

In a temperature range from 20 - 25°C the total development took from 16 - 20 days. The development of the spider eggs under these conditions takes about 20 - 25 days (Table 6; Pl. II). Only in the active larval stage spider eggs are eaten. This stage lasts 2 - 3 days. During this time the larvae consumes on the average 7 spider eggs (min. 5 eggs; max. 13 eggs). This is in agreement with data from the field samples (Table 3).

The development of the larvae in the normal egg sacs and in the glass cages proved to be the same under these temperature conditions. The larvae destroy all the spider eggs in the egg sac. If not all eggs are eaten, the remaining eggs are smashed by the prepupae. When the imago is ready to emerge it bites a hole in the wall of the egg sac, or emerges out of holes bitten by the mother spider to release the juvenile spiders, even though the latter are not present any more. This phenomenon has not yet been studied in detail.

Table 6. Duration of the stages in the development of *Gelis*

Time in days	Larval stage	Size of the larva in mm	
1 — 3	egg	0.5 x 0.1	Pl. II A1
3 — 4	active larva	0.7 x 0.1 to 1.1 x 0.4	Pl. II A2
5	active larva	1.1 x 0.4 to 3.5 x 1.4	Pl. II B1
6	full grown larva	3.5 x 1.4	Pl. II B2
7, 8, 9, 10	prepupa (silkspinning)		Pl. II C1
10 — 16 — 20	pupa		Pl. II C2
16 — 20	imago		

Behaviour of the spider towards the parasite.

When a *Gelis* female is sitting on a spider egg sac, the spider does not seem to notice: it shows no reaction at all. When a spider meets a moving *Gelis* specimen it is sometimes grabbed, but in all cases observed, the spider immediately released the parasite undamaged. The spider takes care of a parasitized egg sac in a normal way, even when it becomes seriously deformed when the larvae are in the pupal stage. Even in the field one can easily recognize a parasitized egg sac at this stage.

Conclusions

1. On the whole the parasitism by *Gelis* is not very important in reducing natality in *Pardosa* spiders: only 139 egg sacs out of 5116 contained *Gelis* larvae, Table 1. However, in some localities and especially in the second egg sac it can be important; e.g. 42.6% of the egg sacs were found parasitized in a sample of the second egg sac of *Pardosa amentata,* Table 3.
2. The number of parasites emerging from a spider egg sac is dependent on the

size of the egg sac; from 1.8 larvae in the second egg sac of *Pardosa pullata,* containing 16.0 spider eggs, up to 10.3 larvae in the first egg sac of *Pardosa amentata,* containing 65.7 spider eggs, Table 3.

3. The parasite adapts the number of eggs laid to the size of the spider egg sac; regulation of the numbers of parasites is therefore determined by the female parasite and not by competition between larvae (conclusion 2 and table 4).
4. The ratio ♂/♀ does not differ statistically from 1.
5. It is possible, at least under laboratory conditions, to raise the larvae of *Gelis* to the adult stage outside the spider egg sac, provided enough food is presented in the form of spider eggs.
6. A *Gelis* larva needs about 7 eggs of a *Pardosa* spider to complete its development, under laboratory conditions. In the field the spider eggs available to a single *Gelis* larva range from 6.4 to 11.3
7. The development of *Gelis* from egg to the adult stage takes about the same time as, or is somewhat shorter than, the development of the spider eggs into juvenile spiders.
8. No conclusions can be drawn on the hibernation of *Gelis* spec.

Discussion

A number of authors have described the occurrence of *Gelis* spec. in egg sacs of several spider species. A list of reference on all spider parasites is given by Eason et al. (1967). They state that the records of spider parasites mainly consists of brief and incomplete accounts. More recently, Horstmann (1970) extensively studied the ecology of Ichneumon flies in Schleswig-Holstein. He described two species of *Gelis, G. micrurus* and *G. pumilus,* both parasitizing egg sacs of Linyphiid spiders, while *G. micrurus* also parasitizes *Pardosa* egg sacs. Both species have more than one generation per year. *Gelis micrurus* parasitizes Linyphiid egg sacs, when *Pardosa* egg sacs are not available any more. In Linyphiid egg sacs there is one larva (Solitärparasit), whereas in *Pardosa* egg sacs there are more than one (Gregärparasit).

In our study no separate species of *Gelis* are distinguished. It is possible, that some of the differences found must be ascribed to specific differences. The mean number of spider eggs and the mean number of *Gelis* larvae per egg sac were calculated for each sample of egg sacs. A positive correlation between the mean number of these eggs and mean number of *Gelis* larvae per sac was demonstrated in comparing all samples of *Pardosa* egg sacs. Within a sample, however, no correlation between size of the egg sac and number of *Gelis* larvae was found. It is possible to estimate the original number of spider eggs in the parasitized egg sac by the size of the corresponding spider. This might mean that in different *Pardosa* species and in different localities, we are dealing with different *Gelis* species or subspecies, adapted to the size of the spider egg sac which is normally available to them. However, from laboratory experiments there is an indication that *Gelis* individuals bred from egg sacs from one locality and sampled at the same time, deposit more eggs in *Pardosa amentata* egg sacs, with a high number of eggs, than in *Pardosa monticola* egg sacs, with a much lower number of eggs.

The observation of Horstmann that the larvae of *Gelis micrurus* are solitary in the small Linyphiid egg sacs and gregarious in *Pardosa* egg sacs points in the same direction. As indicated by Horstmann, *Gelis micrurus* parasitizes Linyphiid egg sacs when *Pardosa* egg sacs are not available. It is not clear whether one generation of *Gelis micrurus* parasitizing Linyphiid egg sacs and the other generation(s), *Pardosa* egg sacs, or whether there is a gradual shift to other egg sacs.

In this context it is of importance to study the behaviour of *Gelis* spec. in connection with egg sacs of other spider species.

2. **Acolus krygeri** Kieffer

A. Field observations

As already remarked above, *Acolus krygeri* has been found in the Netherlands only on the Frisian island Schiermonnikoog; samples from other Frisian islands were not available and our observations therefore only refer to *Pardosa* species found on that island : *P. nigriceps, P. pullata, P. purbeckensis* and *P. monticola.*

Acolus krygeri is practically restricted to *P. nigriceps* and *P. pullata* as host species (Table 7A). It is seldom found in egg sacs of *P. monticola* and *P. purbeckensis* (Table 7B). *Acolus* seems to be restricted to the typical habitat of *P. nigriceps* on Schiermonnikoog. This is a dense vegetation of *Carex arenaria* and *Salix repens* in a dune area (Vlijm & Kessler-Geschiere, 1967). The data in Table 7A refer to specimens found in this habitat. The data in Table 7B are based on specimens sampled in other habitats, mostly bordering on the habitat of *P. nigriceps.* The data in Table 7 are based on samples from several places on Schiermonnikoog and from several years.

Table 7A. Occurrence of *Acolus* larvae in egg sacs of *Pardosa* species. Samples from the habitat of *P. nigriceps*

Pardosa species	First (1) or second (2) egg sac	Number of egg sacs	Parasitized egg sacs	%
P. nigriceps	1	359	227	63.2
P. nigriceps	2	801	564	70.5
P. pullata	1	22	10	45.5
P. pullata	2	124	57	46.0

Table 7B. Occurrence of *Acolus* larvae in egg sacs of *Pardosa* species. Samples from the typical habitat of the spider concerned

Pardosa species	First (1) or second (2) egg sac	Number of egg sacs	Parasitized egg sacs	%
P. pullata	1	146	11	7.5
P. purbeckensis	1	97	4	4.1
P. monticola	1	50	6	12.0

Table 8 shows the percentages of parasitism in 1968 and 1969 at the same sampling site, both for the first and second egg sacs.

Table 9 shows the differences in percentage of parasitism between sampling sites in 1968 for the second egg sac.

Because of the small numbers of *P. pullata* found in the samples (habitat of *P. nigriceps!),* this could be done only for *P. nigriceps.* It is clear that there are no conspicuous differences in percentages of parasitism, neither between the first and second egg sacs nor in the different localities (sampling sites). These data are confirmed by additional samples of either the first or the second egg sac of *P. nigriceps* from other years.

Number of larvae in the spider egg sac.

Although in several egg sacs all spider eggs were parasitized, this generally is the case with only a portion of the eggs. The non-parasitized eggs develop into young spiderlings in a normal way.

There is a relation between the size of the spider egg sac and the number of parasites found (Table 10), which is especially clear for the second egg sac. It is striking, that although the mean number of spider eggs in the first egg sac is much higher than in the second, the mean number of parasites is the same for both egg sacs: about 10. This means that in the first egg sac about 30% of the spider eggs is parasitized, whereas in the second egg sac this percentage is about 60% (Table 11). This is also found for egg sacs of *Pardosa pullata* (Table 11), although the percentage of parasitism in the samples is much lower here: about 45% (Table 7A). If we compare all samples of second egg sacs of *Pardosa nigriceps* with a degree of parasitism lower than 70%, with the samples where the percentage of parasitism is higher, we see that a lower percentage of parasitism results in a lower mean number of parasites per egg sac (Graph 1).

Table 8. Differences in percentage of parasitism in egg sac samples of *Pardosa nigriceps* on the same sampling site in 1968 and 1969

	First egg sac		Second egg sac	
	N	%	N	%
1968	85	63.5	70	78.6
1969	53	64.2	21	61.9

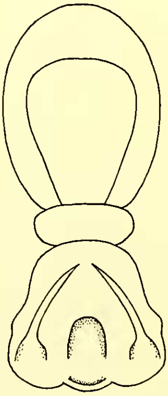


Fig. 2. First stage larva of *Acolus krygeri*

However, the difference is not very conspicuous. The number of parasites in parasitized egg sacs ranges from 1 to 42. The frequencies are given in Graph 2. It is clear from this figure, that the same mean number of parasites in the first and second egg sac is reached

Table 9. Differences in percentage of parasitism in the second egg sac of *Pardosa nigriceps* on several sampling sites

Sampling site	Number of egg sacs	Percentage of parasitized egg sacs
1	70	78.6
2	60	60.0
3	47	76.1
4	30	70.0
5	54	77.8
6	51	74.5
7	55	69.1
8	41	82.9
9	41	92.9

Table 10. Relation between size of the egg sac (number of eggs per egg sac) and the number of parasites per egg sac for *Pardosa nigriceps;* A, data on first egg sac, B, second egg sac

A

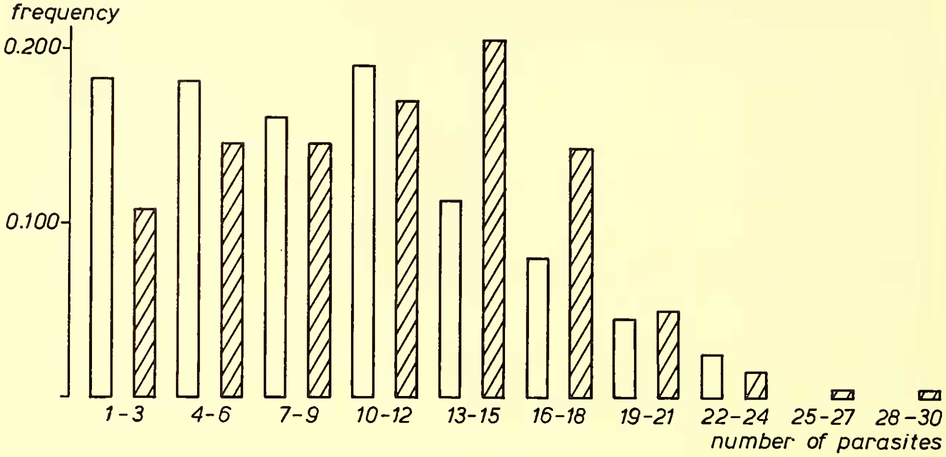
size of the egg sac (number of spider eggs)	4-6	7-9	10-12	13-15	16-18	19-21	22-24	25-27	28-30	31-33	34-36	37-39	40-42	43-45	46-48
mean number of parasites per egg sac						7.8	10.6	8.0	9.3	9.8	10.8	9.6	12.3	12.8	23.4
N						5	10	27	42	54	38	28	12	6	5
% parasitized eggs in the egg sac						39.0	46.0	30.8	32.1	30.6	30.9	25.3	30.0	28.8	49.8

B

mean number of parasites per egg sac	3.6	5.8	6.6	8.7	10.4	11.9	14.1	15.3	16.0
N	5	12	60	114	151	117	70	26	8
% parasitized eggs in the egg sac	72.0	72.5	60.0	62.2	61.2	59.5	61.3	58.8	55.2

Table 11. Mean number of spider eggs and mean of *Acolus* larvae per egg sac in first and second egg sacs of *Pardosa nigriceps* and *Pardosa pullata* from one sampling site

Host species	First or second egg sac	N	Mean number of spider eggs in the egg sac	Mean number of parasites in parasitized egg sacs	N	% of parasitized eggs in the egg sac
P.nigriceps	1	359	32.0 ± 6.01	9.9 ± 6.94	227	30.9
P.nigriceps	2	801	17.0 ± 4.65	10.4 ± 5.67	564	61.2
P.pullata	1	22	30.0 ± 5.65	10.7 ± 3.11	10	35.6
P.pullata	2	124	17.1 ± 5.12	8.6 ± 5.59	57	50.6



Graph 1. Frequency distributions of number of parasites (*Acolus*) per egg sac in samples with a degree of parasitism less than 70% (white: N = 183; M = 9.2 ± 5.76) and samples with a higher degree of parasitism (hatched: N = 894; M = 11.0 ± 5.54)

in a similar way. It seems that it is not so much dependent on the size of the egg sac, but on other phenomena. In Graph 3 the frequencies of the parasitized egg sacs are compared with the frequencies of the total number of parasitized and non-parasitized egg sacs together. Within the groups of first or second egg sacs there is an even chance for every egg sac, not dependent on size, to become parasitized. *Acolus,* therefore, does not seem to discriminate between large and small egg sacs.

In about 20 cases a spider egg appeared to contain 2 larvae of *Acolus,* this is a very low percentage: about 0.5%.

Laboratory observations

Sex ratio.

To determine the sex ratio of *Acolus* two samples of *Pardosa nigriceps* second egg sacs were collected in the field. The spiders with egg sac were kept separately in glass tubes. After emergence the parasites were collected and counted. The results are shown in table 12. There is a dominance of females over males. This ratio fluctuates when we consider the numbers of parasites emerging from an egg sac. When there are only a few parasites in the egg sac the males predominate (Table 13).

Mating occurs within a day after emergence. The parasites were provided with water and honey; it is not clear whether the females need food to develop the eggs. In other experiments, where no honey or sugar were provided the females were able to parasitize spider eggs succesfully.

Parasitizing of the egg sac.

A female spider with a fresh egg sac was put in a glass tube, together with some female *Acolus* specimens, which had already mated. When the egg sac comes in reach of the parasite, the animal takes a crouching position with bent hind legs. This reaction can also be provoked by approaching the animal with the tip of the finger or a pencil.

It then jumps on the egg sac and walks around, tapping the surface of the egg sac with the antennae. Every now and then it stops and pierces the egg sac with the ovipositor (Pl. III Fig. A1). The length of the ovipositor is only 0.4 mm, the spider eggs have a diameter of 1 mm or more, consequently only spider eggs at the surface of the egg sac are within reach of the parasite. After 10-30 minutes the parasite leaves the egg sac and walks around in the glass tube, after which it may again jump on the egg sac. This is the more easily observed when the egg sac is removed from the female spider and thus stays in the same place.

Table 12. Number of males and females of *Acolus* emerged from egg sacs of *Pardosa nigriceps*

Sample	Number of egg sacs	Number of males	Number of females	Ratio ♂/♀
1	28	105	212	0.495
2	20	49	105	0.467

In this way egg sacs of *Pardosa nigriceps* as well as those of *Pardosa amentata* were succesfully parasitized. All egg sacs less than 5 days old, were succesfully parasitized; in two cases where the parasite was apparently parasitizing egg sacs of 7 and 10 days old, no parasites emerged.

Development of the *Acolus* larvae.

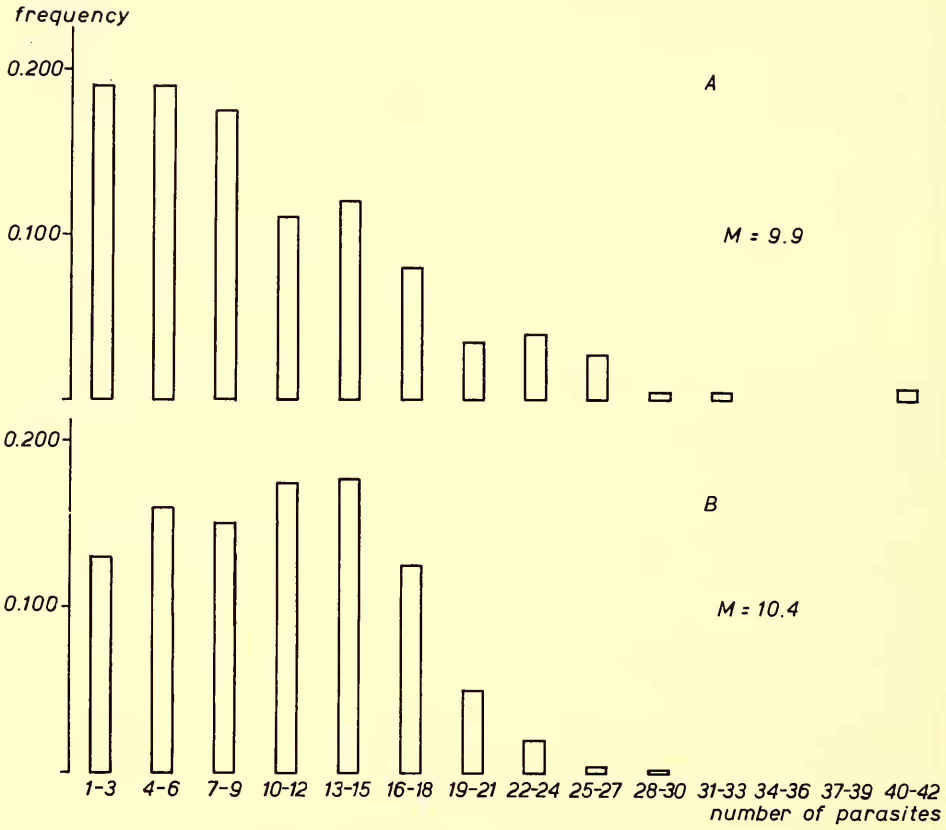
The embryonic development of the parasites was studied by immersing the parasitized spider eggs in paraffin oil, following the technique by Holm (1940) for observing the development of living spider embryos. The egg membrane becomes transparent which makes the larvae of the parasite easily visible.

Controls were made by opening parasitized spider egg sacs of the same age and studying the parasitized eggs in alcohol. The paraffin oil proved to have no effect on the embryonic development of the larvae. At temperature conditions of 25°C the total development took 18-21 days in the following scheme:

day 1 - 3	egg	stage	
day 4	1st	stage larva	pl. III A2
day 5	2nd	stage larva	pl. III B1
day 6 - 7	3d	stage larva (prepupa)	pl. III B2
day 8 - 21		pupa	

During the first 3 days no details in the development of *Acolus* could be observed with the techniques used. The first stage larvae have a curious shape (Fig. 2), probably adapted to floating in the fluid of the spider egg. The active larval stage takes only two days, during which time most of the contents of the spider egg are eaten by the larva. After this active stage the larva becomes immobile; then follows the prepupal and pupal stages in which no clear observations on the development could be made. The longevity of the adult under laboratory conditions was about 14 days.

The influence of different temperatures upon the length of the larval development is shown in table 14. Compared with the development of the spider embryos the development of *Acolus* is short. The total number of parasites out of 20 experimental egg sacs was 174, a mean of 9.1 parasites per egg sac.



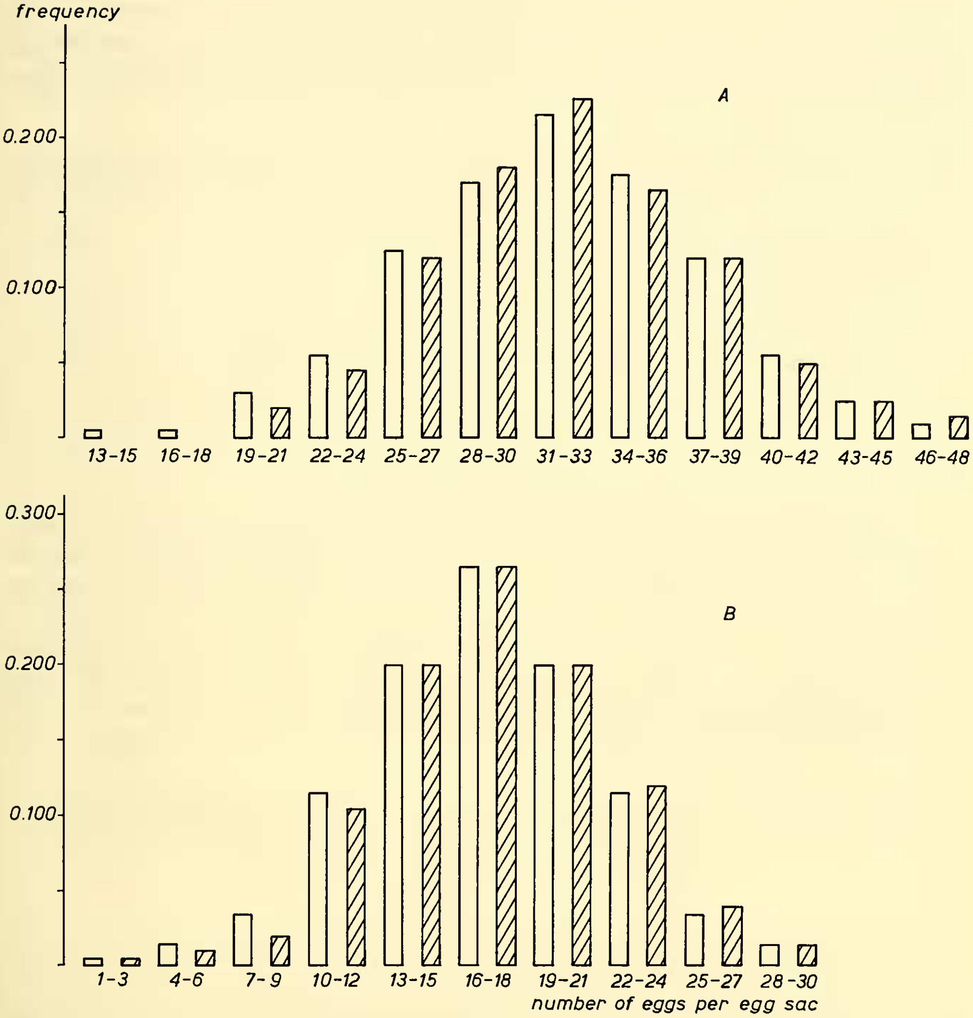
Graph 2. Frequency distributions of the number of parasites per egg sac in A : the first egg sac and B : the second egg sac of *Pardosa nigriceps*

Number of larvae per female parasite.

To learn about the egg-potential of *Acolus,* 35 female spiders with a fresh egg sac were put separately in glass tubes, each with a female *Acolus.* This resulted in a mean number of 11.7 parasites per egg sac emerging from 35 egg sacs (minimum 1, maximum 28). The mean number of spider eggs in these egg sacs was 16.4. The frequency is shown in Graph 4.

Actual time of parasitizing in the field.

During the period of time when female *Pardosa nigriceps* construct egg sacs some samples were taken to determine the actual time of parasitizing of the egg sacs in the field. Table 15 gives the results. On June 2, when only a fraction of the spiders had their egg sacs already constructed, the percentage of parasitism was relatively low. Very soon afterwards the percentage of parasitism reached a maximum. The mean number of parasites per egg sac in the samples was fairly constant.



Graph 3. Frequency distributions of number of eggs per egg sac: white: parasitized and not-parasitized egg sacs together, hatched: parasitized egg sacs; A = first egg sac, B = second egg sac of *Pardosa nigriceps*

Conclusions

1. The occurrence of *Acolus krygeri* on the Frisian island Schiermonnikoog is practically restricted to the habitat of *Pardosa nigriceps:* low dunes with a dense vegetation of *Carex arenaria.*

2. In this habitat *Acolus* is able to parasitize both the first and second egg sacs of *P. nigriceps* for about 70%. For the second egg sac of *P. pullata* this percentage is only about 45%.

3. The mean number of parasites in a parasitized egg sac is about 10. This means that

in the first egg sac of *P. nigriceps* about 30% of the spider eggs in a parasitized egg sac contain larvae of *Acolus,* in the second egg sac this percentage is about 60%.

4. As a result of parasitism the first egg sac of *P. nigriceps* yields on the average about 75% of the potential number of spiderlings. For the second egg sac this percentage is about 60%.

Table 13. Ratio ♂/♀ arranged following the number of specimens emerging from one egg sac. The samples are the same as in table 12

Number of parasites emerging	Sample 1 ratio ♂/♀	N	Sample 2 ratio ♂/♀	N
1 — 5	1.667	26	0.941	33
6 — 10	0.238	8	0.889	17
11 — 15	0.427	157	0.327	65
16 — 20	0.537	126	0.300	39

Discussion

Although there is a wider range of data on *Acolus krygeri,* the relationship between *Acolus* and *Pardosa* remains obscure. No data on the relation between *Acolus* and *Pardosa* are available in literature. It is not clear in the first place whether an egg sac is parasitized only once or more than once by one or by more females of *Acolus.* Considering the results shown in Graph 4 it is evident that one female *Acolus* is able to lay up to 28 eggs (in other experiments even 44 eggs) in one egg sac, but in some cases it parasitizes not more than a single spider egg in an egg sac. These data can explain the wide range of number of parasites per egg sac found in the field.

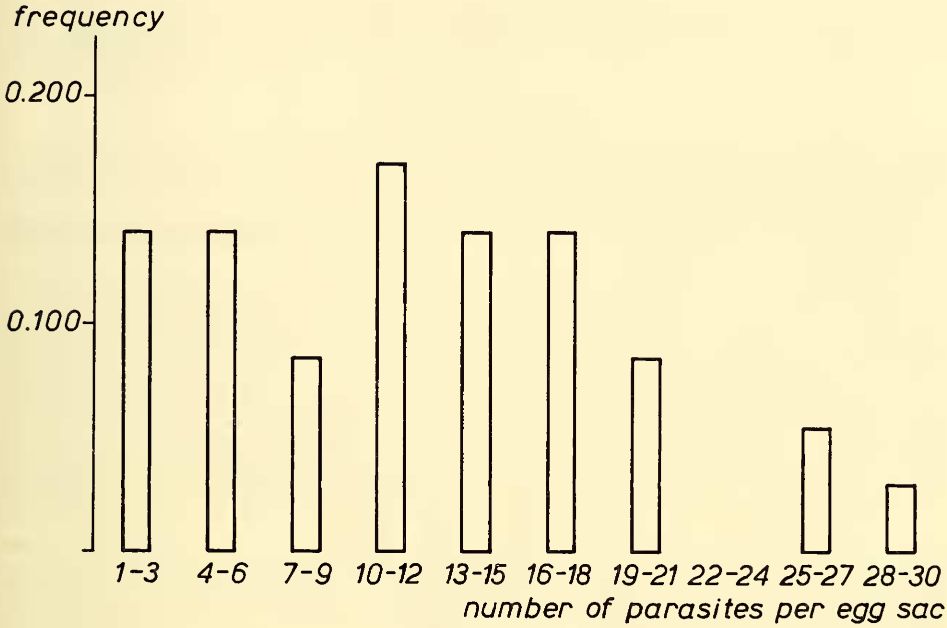
Table 14. Length of development of *Acolus* larvae under different temperature conditions

Temperature	Length of development in days
20°C	25 — 28
25°C	18 — 21
30°C	12 — 14
35°C	8

Parasites apparently may discriminate (cf. Salt, 1936) between parasitized and unparasitized hosts. If this is true for *Acolus* then the parasite may consider an egg sac with some parasitized eggs unsuitable and pay no further attention to it. However, it is also possible that the parasite distinguishes only between parasitized and nonparasitized eggs. In that case an egg sac with a few parasitized eggs can be parasitized again by another parasite.

If egg sacs can be parasitized more than once, this may be expected to happen especially when the density of parasites is highest. The data in Graph 1 suggest that in samples with a high degree of parasitism, probably due to a high density of parasites, the egg sacs are parasitized more often than in samples with a relatively low percentage of parasitism. This results is a higher mean number of parasites per egg sac in the former case.

Another problem arises from the fact that sometimes all or nearly all spider eggs in an egg sac are parasitized. The length of the ovipositor is only 0.4 mm, while the spider eggs measure at least 1 mm. If the eggs are laid directly in the spider eggs, only eggs near the surface of the egg batch can be reached. There are, however, so many egg sacs with all spider eggs parasitized (in the second egg sac of *P. nigriceps* in about 5% of all the cases all eggs are parasitized; in about 10% of the cases all eggs minus 1 are parasitized), that another possibility must be thought of. The explanation might be that the ovipositor is extendable during egg-laying. Or the parasite eggs are laid in or on the egg sac and the larvae crawl inside the egg sac and so settle in a single egg. This latter assumption, however, is highly improbable. In the laboratory experiments the spider eggs were removed from the egg sac immediately after parasitizing and put in paraffin oil. Nevertheless these eggs produced full-grown parasites.



Graph 4. Frequency distribution of number of parasites per egg sac (explanation in text)

When all samples are considered together, no distinct differences in mean number of parasites per spider egg sac become apparent. No simple explanation can be given for this. We know that the population of parasites is able to attack 60 - 80% of the spider egg sacs, while they deposite on the average 10 eggs in an egg sac. Furthermore there is evidence, both from field and laboratory observations, that *Pardosa* egg sacs can only be parasitized when they are not more than a few days old. Probably the period during which spider eggs can be parasitized is the limiting factor. However, it cannot yet be understood how this operates in detail.

More data on density of host and parasite are not yet available. In this context it is

Table 15. Percentage of parasitism of *Pardosa nigriceps* egg sacs by *Acolus*. The samples were taken on the same sampling site

Date	Sample size	Number of parasitized egg sacs (between brackets: %)	Mean number of parasites per parasitized egg sac
2-6-70	23	7 (30.4)	9.9 ± 7.95
4-6-70	14	9 (64.3)	8.4 ± 7.25
5-6-70	25	16 (64.0)	10.3 ± 5.19
9-6-70	17	13 (76.5)	12.9 ± 7.66
15-6-70	41	29 (70.7)	11.1 ± 8.07

important that the locomotory activity of female *Pardosa* after egg sac construction is considerably lower than before (Vlijm & Richter, 1966).

Eason et al. (1967) describe an egg parasite: *Idris* spec. (Hymenoptera, Scelionidae) reared from *Pardosa lapidicina* egg sacs.

The incidence of parasitized eggs in the egg sacs ranged from 63% to 94%, an average of 28 parasites per egg sac, which averaged 35 spider eggs. The parasites only attacked egg sacs that were less than 72 hours old and could not be induced to oviposit in a second egg sac. Moreover this parasitie could not be induced to oviposit in the egg of any spider other than *Pardosa lapidicina,* not even in those of its congener, *P. milvina.* The larval development of the parasite took 21 to 22 days, which coincided with the length of time that the eggs and first instar spiderlings of *Pardosa lapidicina* remain in the egg sac. The parasites were dependent on the female spider as it had to open the egg sac, otherwise the parasites could not emerge. The authors state: "Presumably most or all of the eggs on the periphery of the mass, those that touch the egg sac covering are parasitized, and those in the centre are spared probably due to the limitation in length of the parasite's ovipositor".

Although there is a general resemblance with our observations on *Acolus krygeri,* there are many differences. A coincidence is that *Idris* spec. as well as *A. krygeri* in general do not parasitize all spider eggs in an egg sac. Eason (1966) established that the female *Pardosa lapidicina* tends to destroy her egg sac at the end of the incubation period if no living spiderlings are ready to emerge. In that case it is important for the parasite to leave part of the spider eggs untouched.

The behaviour of *Pardosa nigriceps* and *P. pullata* towards their egg sac seems to be different from that of *P. lapidicina.* If no living spiderlings emerge at the proper time, the egg sac is abandoned; the parasites can emerge then by biting holes in the wall of the sac.

3. The occurrence of *Acolus krygeri* and *Gelis* spec. together

In 1968 a number of egg sacs were collected, that contained *Acolus krygeri* and *Gelis* spec. together. In total 15 egg sacs (9 of *P. nigriceps* and 6 of *P. pullata*) contained *Gelis* larvae. Ten of these (66.7%) contained both *Gelis* and *Acolus* larvae. The mean number of *Gelis* larvae per egg sac was 1.9, the mean number of *Acolus* larvae was 11.5. In the egg sacs with *Gelis* larvae alone the mean number of larvae was 2.2. No spiderlings were found in the egg sacs. As indicated before, the mean number of larvae in egg sacs with *Acolus* alone is about 10.

Conclusions

1. In the group of egg sacs parasitized by *Gelis* the percentage of parasitism by *Acolus* is comparable with the percentage of parasitism in the whole of egg sacs. This means that *Gelis* is not able to recognize an egg sac already parasitized by *Acolus,* or vice versa.

2. It seems that the larvae of *Gelis* cannot consume spider eggs already parasitized by *Acolus,* for when there were spider eggs left in the sacs, these were in all cases parasitized by *Acolus.*

GENERAL DISCUSSION

Some aspects of the biology of both parasites (*Gelis* and *Acolus*) had little or no attention in our studies. Problems of hibernation, density and the successive generations have not been dealt with. "The wealth of material concerning spider parasites is composed principally of brief and incomplete accounts which are widely scattered in the literature" (Eason et al., 1967).

The present study as a whole can be seen as an attempt to study the relation between egg parasites and spiders more closely. This is only possible when there is at least a substantial knowledge about the biology of one of the partners in this relationship. In our department much work has been done on the biology of *Pardosa* spiders, and therefore, from our knowledge of spider species, we gained some insight in the biology of the parasites. It is evident that knowledge about spider parasites may help to understand the biology of the spiders.

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